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Reappraising the voices of wrath

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Abstract

Cognitive reappraisal recruits prefrontal and parietal cortical areas. Because of the near exclusive usage in past research of visual stimuli to elicit emotions, it is unknown whether the same neural substrates underlie the reappraisal of emotions induced through other sensory modalities. Here, participants reappraised their emotions in order to increase or decrease their emotional response to angry prosody, or maintained their attention to it in a control condition. Neural activity was monitored with fMRI, and connectivity was investigated by using psychophysiological interaction analyses. A right-sided network encompassing the superior temporal gyrus, the superior temporal sulcus and the inferior frontal gyrus was found to underlie the processing of angry prosody. During reappraisal to increase emotional response, the left superior frontal gyrus showed increased activity and became functionally coupled to right auditory cortices. During reappraisal to decrease emotional response, a network that included the medial frontal gyrus and posterior parietal areas showed increased activation and greater functional connectivity with bilateral auditory regions. Activations pertaining to this network were more extended on the right side of the brain. Although directionality cannot be inferred from PPI analyses, the findings suggest a similar frontoparietal network for the reappraisal of visually and auditorily induced negative emotions.

Key words: reappraisal; vocal emotions; prosody; fMRI; psychophysiological interaction

Introduction

Emotions constitute powerful reactions to specific events or thoughts. They can be lifesaving, allowing, e.g. someone to quickly freeze or flee when faced with threatening environmental events (Dalgleish, 2004). When individuals are confronted with a choice, emotions and their associated physiological signals ('somatic markers') support decision-making (Damasio, 1996). However, emotions can also constitute maladaptive responses that need to be modified, reduced or amplified in everyday contexts. Adults have acquired strategies for actively controlling, i.e. suppressing or amplifying, their emotional reactions. Because of the relevance of these strategies to mental health (Gross and Levenson, 1997), numerous studies have recently started investigating the neural correlates of emotion regulation strategies by using electroencephalography (Hajcak *et al.*, 2006; Korb *et al.*, 2012) and brain imaging (e.g. Beauregard *et al.*, 2001; Ochsner *et al.*, 2002; Vrtička *et al.*, 2011). One of the most studied forms of emotion regulation is reappraisal, in which the perceiver changes his/her interpretation of a stimulus or event and thus changes its emotional impact on the self (Gross, 1998). Through reappraisal, the impact of a negative event can be diminished by imagining one's situation to get better, or by viewing the event from a more detached perspective. Reappraisal can also be used to increase one's emotional reactions; in some cases, this might even be desirable in response to negative events. For example, athletes may want to up-regulate negative emotions to ramp up aggression before a big game.

In general, brain-imaging studies indicate that reappraisal recruits frontal regions [e.g. the dorsomedial and dorsolateral prefrontal cortex (PFC); the anterior cingulate cortex (ACC)] and posterior parietal regions to up- or down-regulate emotional responses and neural activity in brain areas known for their emotional processing, such as the amygdala, the insula or the basal ganglia (Ochsner and Gross, 2005, 2008; Wager *et al.*, 2008;

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Buhle *et al.*, 2013; Kohn *et al.*, 2014). Moreover, the functional coupling between prefrontal areas and the amygdala has been shown to increase during reappraisal (Banks *et al.*, 2007). Nevertheless, some variability in this neural circuitry has also been found across studies, possibly depending on differences in the experimental design, such as stimulus duration (Kalisch, 2009). Moreover, even though up- or down-regulating of emotions recruits a common network of regions in the PFC and ACC, these reappraisal strategies may rely in part on different neural structures. To the best of our knowledge, only three functional magnetic resonance imaging (fMRI) studies have reported the results of comparing reappraisal to increase and to decrease negative emotions. Of these, two reported greater activity during reappraisal to 'increase' negative emotions in regions of the 'left' rostromedial PFC, such as the inferior frontal gyrus (IFG), the medial frontal gyrus (MFG) and the superior frontal gyrus (SFG) (Ochsner *et al.*, 2004; Urry *et al.*, 2006). One of these studies also reported that reappraisal to 'decrease' negative emotions was accompanied by greater activity in regions of the 'right' lateral and orbitofrontal PFC, including the SFG, the MFG and the IFG (Ochsner *et al.*, 2004). Finally, the third study reported somewhat bilateral PFC activation, which was greater during reappraisal to increase negative emotions than to decrease them (van Reekum *et al.*, 2007). On the limited basis of the current literature, it can be assumed that reappraisal to increase negative emotions will recruit mostly the left PFC, while reappraisal to decrease them will result in greater activation of the right PFC. However, more research is needed to directly compare the neural correlates of reappraisal to increase *vs* to decrease negative emotions. This study aimed at filling this gap in the literature.

Another limitation of the extant literature on the neural correlates of reappraisal is that nearly all brain imaging studies have so far used only 'visual' stimuli. A typical experiment of this kind uses negative International Affective Picture System (IAPS) pictures (Lang *et al.*, 1999) in order to elicit emotional responses, which then have to be modulated via reappraisal. Little is known; however, about the cerebral areas involved in the reappraisal of emotions elicited through other sensory modalities, such as touch, olfaction, taste and audition. For example, of the 13 fMRI studies reviewed by Kalisch (2009), none investigated reappraisal using stimuli other than emotional photos or videos; although two of the reviewed studies used pain, or the anticipation of pain, they did not specifically investigate reappraisal. Similarly, another review (Buhle *et al.*, 2013) identified 48 fMRI studies on reappraisal, of which 41 used photos or videos as stimuli. Of the remaining seven studies, one had participants remember arousing and negative autobiographical events (Kross *et al.*, 2009), and another used standardized scripts from a database (Lang *et al.*, 2012), which may have included memories of, or references to, auditory stimulation, although this aspect was not mentioned. In summary, most, if not all, brain imaging studies on the neural correlates of reappraisal have so far exclusively used visual stimuli to induce emotions in participants.

Importantly, and to the best of our knowledge, the brain activity accompanying the regulation of 'auditorily' induced emotions has never been investigated. This is regrettable, since in everyday life, people can be exposed to emotional stimuli that are, e.g. of a purely auditory nature (imagine arguing with somebody over the phone), or which are of a combined visual and auditory nature. The neural correlates of emotions induced via auditory stimulation may differ from those relating to visual stimulation. For example, the amygdala is commonly activated when emotional stimuli are presented visually, but less so when they are presented auditorily (Costafreda *et al.*, 2008). Moreover, amygdala responses habituate rapidly, and in the absence of salient visual stimuli, even threatening contexts can result in reduced instead of increased amygdala activation (Lindquist *et al.*, 2012). Because of these and other findings (see below), the role of the amygdala in the emotional response to auditory stimuli remains debated. This leads to the possibility that emotion regulation areas may also differ, depending on whether emotions are induced through visual stimuli or through auditory stimuli. It is thus of great scientific interest to investigate the neural correlates of the reappraisal of auditory stimuli and to test whether they resemble, or differ from, those underlying the reappraisal of visually evoked emotions.

The study of the neural correlates of emotional reactions evoked from auditory stimuli and of emotion regulation in response to these stimuli may also be of clinical interest, as it could contribute to the understanding of auditory hallucinations. Individuals with schizophrenia have abnormal emotional perception, experience and expression (Aleman and Kahn, 2005) and can suffer from auditory hallucinations (Lennox *et al.*, 2000). Auditory hallucinations in schizophrenia occur via the activation of auditory regions in the absence of an auditory stimulus and are accompanied by abnormal activation of the amygdala and parahippocampal gyrus (Escartí *et al.*, 2010). Evidence suggests that people with schizophrenia have impaired emotion regulation capacities, which may hinder coping with their hallucinations and other psychotic symptoms (Badcock *et al.*, 2011). Therefore, understanding the neural mechanisms underlying the reappraisal of auditorily induced emotions is likely to stimulate the development of better treatment of auditory hallucinations in schizophrenia.

Emotions in voices are largely conveyed via suprasegmental features of speech, such as its fundamental frequency (F0; mostly contributing to pitch) and amplitude (mostly contributing to loudness perception), as well as other features (e.g. harmonics-to-noise ratio) that are related to voice quality (Banse and Scherer, 1996). These emotional intonations embedded in speech are commonly referred to as emotional prosody. The perception and discrimination of emotional prosody may accelerate the perceiver's heart rate (Kreibig, 2010; but see Aue *et al.*, 2011) and predominantly, but not exclusively, recruit the activity of a mostly right-sided frontotemporal cortical network, including the superior temporal gyrus (STG), the superior temporal sulcus (STS), the IFG and the orbitofrontal cortex (OFC) (Grandjean *et al.*, 2005; Sander *et al.*, 2005; Schirmer and Kotz, 2006; Frühholz and Grandjean, 2012). In addition, some studies have reported increased activation of subcortical structures such as the amygdala, the thalamus and the basal ganglia (Grandjean *et al.*, 2005; Sander *et al.*, 2005; Wiethoff *et al.*, 2009; Leitman *et al.*, 2010; Frühholz and Grandjean, 2013a). However, the involvement of the amygdala in the decoding of emotional prosody remains debated, since amygdala lesions often do not affect auditory emotion recognition (Adolphs and Tranel, 1999; Anderson and Phelps, 2002; Mitchell and Bouças, 2009; Bach *et al.*, 2013), and increased amygdala activation is rarely reported in response to vocal emotional stimuli in brain-imaging studies (Buchanan *et al.*, 2000; Wildgruber *et al.*, 2002, 2005; Kotz *et al.*, 2003, 2013; Pourtois *et al.*, 2005; Ethofer *et al.*, 2006; Wiethoff *et al.*, 2008; Szameitat *et al.*, 2010; Escoffier *et al.*, 2013). Interestingly, amygdala activation in response to emotional vocalizations was found in expert meditation practitioners generating a loving-kindness-compassion meditation state (Lutz *et al.*, 2008), suggesting that practicing meditation, and, speculatively, also reappraisal or other forms of emotion

regulation, can result in heightened amygdala responses to auditory emotional stimuli.

In this study, we investigated whether the neural circuitry underlying the reappraisal of emotions elicited through visual stimuli is also recruited during reappraisal of emotions elicited through auditory stimuli. In order to induce negative emotions in participants, auditory voice stimuli spoken with an angry prosody were used. Neutral prosody served as control. In order to eliminate semantic understanding, all voice stimuli were in Italian, and participants were French speakers with no knowledge of Italian. Moreover, to provide a semantic context for the auditory stimuli, and thus to facilitate reappraisal, all auditory stimuli were preceded by neutral written scenarios. We investigated changes in heart rate, brain activity and subjective feeling accompanying the processing of angry prosody and that were, across two reappraisal conditions, associated with emotion regulation of auditorily induced emotions. Auditory instead of visual emotional stimuli were specifically chosen because their presentation commonly leads to cortical activations without consistently involving emotion-eliciting centers such as the amygdala. Indeed, the fact that the neural circuitries underlying emotional responses to auditory and visual stimuli may differ suggests that differences may also exist between these two stimulus modalities when it comes to emotion regulation.

Listening to angry *vs* neutral prosody was expected to result in greater felt negative emotion and increased activity in the STG, STS, IFG and OFC, especially on the right side (Schirmer and Kotz, 2006; Frühholz and Grandjean, 2013b,c). Neural responses to angry prosody were also assessed in the amygdala by using a region of interest (ROI) approach. From a review of the literature on psychophysiological responses to emotional stimuli in general (Kreibig, 2010), we hypothesized finding a higher heart rate in response to angry prosody than to neutral prosody, although null findings have also been reported, specifically for angry prosody (Aue *et al*., 2011).

Reappraisal of negative emotions elicited through visual stimuli has repeatedly been shown to recruit lateral and medial prefrontal cortices, as well as parietal areas (Kalisch, 2009; Buhle *et al*., 2013). The frontal structures that are active during reappraisal also underlie cognitive processes taking place during other cognitive control tasks that do not involve emotional stimulation (Ochsner and Gross, 2005). Therefore, we expected prefrontal, but also parietal areas, to be more active during reappraisal than during passive listening to angry prosody. More specifically, we expected greater activation of the left rostromedial PFC during reappraisal to increase negative emotions, and increased activation of the lateral and orbitofrontal PFC, especially on the right side, during reappraisal to decrease negative emotions (Ochsner *et al*., 2004; Urry *et al*., 2006).

In addition to the classical peak analysis of fMRI data, we also performed psychophysiological interaction (PPI; Friston *et al*., 1997) analyses to study the task-dependent coupling between specific volumes of interest (VOIs) and the rest of the brain. Moreover, the location of voice-selective areas was assessed in each participant by using a standardized localizer task (Belin *et al*., 2000).

Materials and methods

Participants

Twenty healthy participants were recruited through announcements on campus. They were all native or fluent French speakers with no knowledge of Italian, and they had normal or corrected to normal vision, no auditory impairments and no known neurological disorders. Participants were paid for their participation. MRI data had to be excluded from two participants because of head movement. The results reported herein are based on the analysis of the remaining 18 participants (10 females, mean age = 27 years, range = 20–46). As a result of technical problems, ratings of felt negative emotion were recorded for only 10 of these 18 participants (3 females), and heart rate data were available for only 16 participants (8 females). All participants provided written informed consent. The study was approved by the local ethics committee.

Stimuli

Stimuli of the voice localizer task consisted of vocal and non-vocal sounds of different origin, normalized for energy levels, and presented in 40 blocks of 8 s (Belin *et al*., 2000).

The 80 trials of the main task comprised unique combinations of visual and auditory stimuli, which varied across participants. Even though we were interested in the emotional response and the reappraisal of emotional prosody, we decided to present a visual stimulus before every auditory stimulus, consisting of a short scenario (one or two sentences, see Appendix), written in black text on a grey screen. The scenario was intended to provide participants with a situational context, which was necessary for reappraisal of emotions because auditory stimuli were spoken in Italian and thus had no semantic content for our French-speaking participants. Auditory stimuli were voices (50% men) spoken in Italian with neutral ($n = 20$) or angry prosody ($n = 60$). All voice stimuli were extracted from movie scenes obtained from the Internet or from DVDs, cut to a length of 6 s, and equalized for mean energy by using the software Praat (http://www.fon.hum.uva.nl/praat/). All scenes were either originally in Italian, or dubbed into the Italian language, and were free of background noise. Italian voices were chosen to minimize semantic effects in our sample of French speakers. Four examples of the audio stimuli can be found at https://www.youtube.com/playlist?list=PLizG–jbGGnXb_eJExbUwhJFKQb6XdV8A.

Voice stimuli were selected from a larger pool from the results of a separate rating study. A separate group of 20 participants (eight men; mean age = 30 years, no knowledge of Italian) rated 75 angry and 20 neutral voice vocalizations on two Likert scales of 100 points each. The ratings for each stimulus were perceived anger (how much anger did the voice express?) and felt arousal (how much were you aroused by the voice?). Instructions specifically asked participants to imagine that the voice was addressed to them. Results showed higher ratings for angry voices on both scales. Of these 95 stimuli, we discarded the 15 angry voices having received the lowest ratings and kept the remaining 60 angry and 20 neutral voices, which were subsequently used as stimuli in the fMRI task. As tested with independent-samples two-tailed *t*-tests, ratings of perceived anger were significantly higher [$t(63.23) = 25.67$, $P < 0.001$] for angry ($M = 60.82$, s.d. = 16.74) than for neutral voices ($M = 4.31$, s.d. = 1.87). Similarly, ratings of felt arousal were higher [$t(77.71) = 18.2$, $P < 0.001$] for angry ($M = 27.76$, s.d. = 8.52) than for neutral voices ($M = 5.12$, s.d. = 2.59).

Procedure

A within-subjects repeated measures design was used. Participants read written instructions and practiced the emotion regulation task during three practice trials outside of the

scanner. These trials were not part of the experiment and were identical for all participants. Just before moving participants into the scanner, a plethysmograph clip was attached to the left-hand index finger in order to record blood flow at 2000 Hz (Biopac Systems, Inc.), from which heart rate was deduced. Inside the scanner, participants completed the main regulation task (~30 min), followed by a voice localizer task (passive listening, 13 min) to determine their individual voice-selective areas (Belin *et al.*, 2000). Visual stimuli were projected on a screen seen by participants through a mirror attached to the head coil. Auditory stimuli were presented binaurally via MRI-compatible headphones. Sound volume was individually adjusted for each participant before the beginning of the experiment, so that auditory test stimuli (different from stimuli used in the task) could be heard clearly without being painful.

In the main task (see Figure 1), each trial comprised, in this order, a screen containing a short text to provide a situational context (7 s; see Appendix for all contexts), a blank screen (1.5 s), the auditory stimulus together with the image of a triangle (6 s), a screen asking the participant to rate the intensity of his/her negative emotions (3 s) and a screen with the word 'relax' (variable duration ranging from 4 to 6 s). Ratings were provided by pressing buttons 1 (very low intensity of negative emotions) to 4 (very high intensity of negative emotions) of an MRI-compatible response box. The average trial duration was 22.5 s (range 21.5–23.5 s).

There were three conditions (Feel, Increase, Decrease), which were symbolized by a sideward-, upward- or downward-pointing triangle, respectively, appearing at the same time as the voice stimuli. Participants were instructed to read and vividly imagine the scene described in each context. Moreover, in the Feel condition, they were asked to pay attention to the auditory stimulus while continuing to visualize the context, but without trying to reappraise the situation. In contrast, participants were asked to actively imagine the situation becoming worse in the Increase condition and becoming better in the Decrease condition. For example, when reading 'In the subway, a man turns to you and says' (Scenario 6; see Appendix), and then hearing an angry male voice while receiving instructions to Increase (upward triangle), participants could imagine having inadvertently stepped on the man's foot, or having taken his seat, when entering the subway. This may have led to feelings of guilt, shame or embarrassment. Participants could further up-regulate negative emotions generated by the angry prosody by imagining the man to be big and muscular and to be looking extremely aggressive through his body language, clothing and general appearance. By doing so, participants may have developed feelings of fear and/or aggression in response to the imminent danger of being physically (in addition to verbally) attacked. Neutral prosody occurred only in the Feel condition, and Increase and Decrease trials contained only angry prosody. Importantly, the combinations of contexts and auditory stimuli were presented randomly across participants, the only constraint being that the gender of the voice had to match the gender of the context. The main experiment included 80 trials in semi-random order (with a maximum of three same-condition trials in a row) divided into two sessions and lasted ~30 min.

Image acquisition

Functional imaging data for the voice localizer and the main task were obtained on a 3-T SIEMENS Magnetom Trio System (Siemens, Erlangen, Germany), using a 12-channel head coil and a T2*-weighted gradient echo-planar imaging (EPI) sequence (36 contiguous axial slices aligned to the AC–PC plane, slice thickness 3.2 mm, distance factor 20%, TR = 2.1 s, TE = 30 ms, flip angle = 80°, in-plane resolution 3.2 × 3.2 mm).

A high-resolution magnetization-prepared rapid acquisition gradient echo T1-weighted sequence (192 contiguous slices, TR = 1.9 s, TE = 2.27 ms, TI = 900 ms, flip angle = 9°, FOV 256 × 256, in-plane resolution 1 × 1 mm, slice thickness 1 mm) was obtained in sagittal orientation to obtain structural images.

Data analysis

Participants' ratings were analyzed in a repeated-measures analysis of variance (rmANOVA), with four levels (Feel Negative, Feel Neutral, Increase, Decrease) to compare the amount of felt negative emotion across trials of the four conditions. Bonferroni corrections were applied to *post hoc* tests.

Heart rate data were filtered by applying a 0.5 Hz high-pass filter and a 20 Hz low-pass filter, and peaks (beats per minute) were detected by using Acqknowledge software (www.biopac.com). The 1-s period before stimulus onset was averaged and used as baseline. For each trial, all data points from stimulus onset to the end of stimulus presentation were expressed as percentages of the baseline. For statistical analyses, heart rate during stimulus presentation was averaged over six consecutive periods of 1 s. The effects of emotional prosody and regulation condition were tested in an rmANOVA with the factors Condition (Feel Negative, Feel Neutral, Increase, Decrease) and Time (1–6).

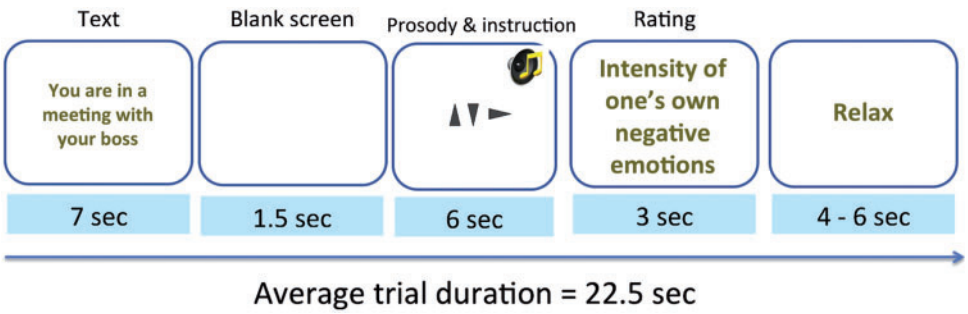

Fig. 1. Depiction of an example trial of the main fMRI task. A written scenario was displayed for 7 s, followed by an auditory stimulus of either neutral or angry prosody. Depending on the condition, angry prosody occurred in combination with an upward, downward or sideward triangle, instructing participants to increase or decrease their emotional response through reappraisal, or to pay attention to it without trying to modify it, respectively. Neutral prosody only occurred in combination with sideward triangles (Feel condition), during which no reappraisal was required. At the end of each trial, participants had 3 s to rate the intensity of their felt negative emotion.

Pre-processing and statistical analysis of the functional images was performed by using the Statistical Parametric Mapping software SPM8 (Welcome Department of Cognitive Neurology, London; http://www.fil.ion.ucl.ac.uk). After motion estimation, functional images were realigned to the mean image of each session and unwarped by using fieldmap scans recorded prior to the main experiment. The anatomical images were coregistered to the functional images. The new segment option in SPM8 was used to segment the T1 anatomical images. Individual DARTEL flow fields were estimated from segmented gray and white matter tissue classes and used for normalizing T1 and EPI images to the Montreal Neurological Institute stereotactic template brain. Normalized images were resampled to $2 \times 2 \times 2$ mm voxel size and spatially smoothed by using a non-isotropic Gaussian kernel of FWHM $8 \times 8 \times 8$ mm to decrease differences in individual structural brain anatomy and to increase the signal-to-noise ratio. A high-pass filter (128 s) was applied to remove low-frequency signal drifts. A first-order autoregressive model served for estimating temporal autocorrelations by using restricted maximum likelihood estimates of variance components.

We used a general linear model for the first-level statistical analyses, including boxcar functions defined by the onsets and durations of the auditory stimuli. These boxcar functions were convolved with a canonical hemodynamic response function. Separate regressors were created for context (7 s), auditory stimulus (6 s; either Feel Negative, Feel Neutral, Increase or Decrease) and rating period (3 s). Six motion correction parameters were included as regressors of no interest to minimize false positive activations due to task-correlated motion. Single-subject contrasts were taken to second-level random-effects analyses to find significant clusters across the subject sample. Functional activations were thresholded, following suggested criteria (Lieberman and Cunningham, 2009), at a voxel size threshold of $P < 0.001$, uncorrected, and a cluster extent of $k = 10$.

PPI (Friston *et al.*, 1997) analyses were computed to estimate which connections between functionally defined VOIs and the rest of the brain were modulated by stimulus valence and regulation condition. PPI analyses investigate task-specific changes in functional connectivity between brain regions. They have become more commonly used in recent years because neuroscientists increasingly think of the brain in terms of networks (O'Reilly *et al.*, 2012). The PPI analysis uses the time course of the functional activity in a seed region to model the activity in other target brain regions. A model is created by multiplying the time course activity in the seed region with a binary comparison of task conditions ('1' and '−1'). If the brain activity in the target region can be explained by the model, functional connectivity with the seed region is assumed.

Six different seed regions were chosen to perform PPI analyses. The right STS (40, −42, 14) and STG (66, −32, 20) regions were chosen because they showed significantly increased activation to angry compared with neutral prosody and because they are known to be part of a network that is relevant to the processing of vocal emotions. Regions of the right and left ACC were used as seeds because they were also significantly activated during angry *vs* neutral prosody and because the ACC can be an emotional-cognitive interface (Paus, 2001). The left SFG (−16, 38, 42) was chosen because it was the only significant cluster in the contrast Increase > Decrease, and it has previously been shown to specifically accompany reappraisal to increase emotions (Ochsner *et al.*, 2004; Urry *et al.*, 2006). Finally, the right MFG (52, 34, 24) was used as a seed region because it was the greatest significantly activated cluster in the Decrease > Increase contrast, and it was also found to be more active during reappraisal to decrease emotion in previous studies (e.g. Ochsner *et al.*, 2004), as well as in recent meta-analyses (e.g. Kalisch, 2009). In each of these four seed regions (right STS, right STG, left SFG and right MFG, a 4-mm radius sphere was placed around the peak voxel, and the time course of activation was extracted for each participant.

Each PPI analysis was set up as a general linear model for one of the four seed regions, including three regressors. The extracted and deconvolved time course of functional activity in a specific seed region (the physiological variable) was used as a first regressor. The second regressor was composed of the comparison between angry and neutral voices during the Feel condition, or the comparison between Decrease and Increase trials, or their reverse (the psychological variable). We thus created a time course regressor for the task, including as many sampling points as for the physiological variable. The values in the second regressor were set to '1' for trials of one condition (e.g. Feel Negative) and to '−1' for trials from the other condition (e.g. Feel Neutral). The third regressor represented the interaction between the first two regressors; it was created by a point-by-point multiplication of the time course for the physiological variable and the time course for the psychological variable. This last regressor was the only regressor of interest, whereas the psychological variable and the deconvolved time course served as regressors of no interest in each PPI analysis. By including the first two regressors, we ensured that the resulting functional activation was solely determined by the interaction between the physiological variable and the psychological variable. In total, eight different PPI analyses were performed by using four seed regions (right STS, right STG, left SFG and right MFG) and four contrasts (Feel Negative > Feel Neutral, Feel Neutral > Feel Negative, Increase > Decrease, Decrease > Increase).

Data from the voice localizer were pre-processed in the same manner as those from the main task. The contrast voice > non-voice was computed across participants in order to determine bilateral cortical voice-selective areas. The significance threshold was set to $P < 0.001$ and a cluster extent of $k = 10$ voxels. From the resulting clusters with peak voxels at +64, −16, −2 and −62, −20, 02, beta values were extracted with the REX script (Duff *et al.*, 2007), averaged over both sessions, and analyzed in an rmANOVA with the factors Condition (Feel Negative, Feel Neutral, Increase, Decrease), and Side (Left, Right). In order to fully test the role of the amygdalae in the emotional response to and the reappraisal of angry prosody, the same kind of rmANOVA was computed with the average beta values from two structurally defined amygdala ROIs.

Results

Ratings

A one-way ANOVA performed on participants' ratings of their felt negative emotion (Figure 2) after each trial resulted in a main effect of Condition [$F(3,27) = 20.8$, $P < 0.001$, $\eta_p^2 = 0.7$]. Bonferroni-corrected *post hoc* tests confirmed that Increase trials ($M = 3$, s.d. $= 0.3$) elicited significantly more negative emotion compared with Decrease trials [$M = 2.4$, s.d. $= 0.4$, $t(9) = 3.9$, $P = 0.02$] and Feel Neutral trials [$M = 1.7$, s.d. $= 0.5$, $t(9) = 7.3$, $P < 0.001$]; felt emotion was also more negative for Feel Negative trials ($M = 2.6$, s.d. $= 0.4$) than for Feel Neutral trials [$t(9) = 4.3$, $P = 0.01$] and for Decrease trials than for Feel Neutral trials [$t(9) = 3.5$, $P = 0.04$].

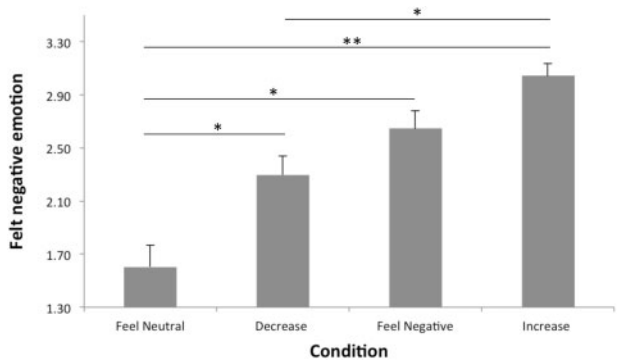

Fig. 2. Mean amplitude (and SEM) of ratings of the intensity of the felt negative emotion, separated by condition. As a result of technical problems, data from only 10 participants were available. *$P < 0.05$, **$P < 0.01$.

Heart rate

Heart rate was averaged over six consecutive windows of 1 s, starting at stimulus onset until end of stimulus presentation, and analyzed in an rmANOVA with the factors Condition (Feel Neutral, Feel Negative, Increase, Decrease) and Time (1–6). This resulted in a significant effect only of Time [$F(5,75) = 5.1$, $P = 0.01$]. Neither the main effect of Condition nor the Condition by Time interaction reached significance ($Fs < 1$, $Ps > 0.4$, ns). Thus, heart rate was not significantly modulated by the stimulus features or by the participants' emotion regulation attempts.

fMRI data

Whole brain analyses

To assess the neural correlates of perceiving angry prosody without attempting to voluntary reappraise it, we contrasted Feel Negative with Feel Neutral trials (Figure 3B and Table 1). This resulted in a number of brain areas showing significantly greater activation to angry than to neutral prosody, such as the bilateral ACC and parietal areas. In agreement with prior studies (Grandjean *et al.*, 2005; Frühholz *et al.*, 2012), the right posterior STS, STG and IFG showed greater activation to angry than to neutral prosody. Anger trials did not result in greater activation of the amygdala.

The contrast Increase *vs* Feel Negative was computed to assess the brain areas showing greater activity when participants reappraised the impact of angry prosody to imagine a worsening of the situation. The only significant cluster was found in the left cuneus (Table 2).

Several clusters were found to be related to participants' reappraisal to decrease the emotional impact of the angry prosody compared with Feel Negative (Figure 3C and Table 3). These clusters included a network of the MFG and inferior parietal cortex, and they were more extended in the right compared with the left hemisphere.

When we compared brain activity specifically related to up- *vs* downregulation of negative emotion, the left SFG showed greater activation during reappraisal to increase than to decrease negative emotion (Figure 3E and Table 4). The opposite contrast, Decrease > Increase (Figure 3D and Table 5), resulted in greater neural activity during Decrease in a bilateral network encompassing the MFG and the inferior parietal cortex (inferior parietal lobule). Clusters in the right OFC and bilateral medial temporal gyrus (MTG) were also found.

ROI analyses

Beta values of the right and left voice areas, which had been identified through the voice localizer, were averaged over both sessions and analyzed in an rmANOVA with the factors Condition (Feel Negative, Feel Neutral, Increase, Decrease) and Side (Left, Right). This resulted in a significant Condition × Side interaction [$F(3,51) = 4.51$, $P = 0.007$, $\eta_p^2 = 0.21$] because of a trend [$t(17) = 2.02$, $P = 0.06$] for greater activation during Increase compared with Feel Neutral in the right voice area. All other effects were not significant (all $Fs < 0.6$, all $Ps > 0.5$).

Beta values of the structurally defined right and left amygdala ROIs were averaged over both sessions and analyzed in a similar rmANOVA. This resulted in a significant Condition × Side interaction [$F(3,51) = 3.00$, $P = 0.04$, $\eta_p^2 = 0.15$] because of non-significantly (all $ts < 1.3$, all $Ps > 0.24$) greater amygdala activation during Feel Negative compared with all other conditions on the left but not on the right side of the brain. There was also a non-significant trend of overall greater amygdala activity on the left side [$F(1,17) = 3.63$, $P = 0.074$, $\eta_p^2 = 0.18$].

Psychophysiological interaction

To investigate the connectivity patterns of brain regions showing significantly increased activity in our experimental design, we created VOIs by placing 4-mm radius spheres around the peak voxels of selected clusters emerging from the contrasts Feel Negative > Feel Neutral, and Increase > Decrease. These VOIs were used as seed regions for PPI analyses (see Figure 4 and Tables 5–7).

A first PPI analysis focused on the connectivity pattern arising from areas implicated in the processing of and the emotional response to angry prosody. We used as VOIs the right STS and STG, as well as bilateral ACC regions (see earlier, Figure 3B and Table 1) and tested their whole-brain functional connectivity in the Feel Negative > Feel Neutral contrast. We found greater functional connectivity during Feel Negative trials between the right STS (40, −42, 14) and the right parietal cortex and the MFG, and inverse connectivity between the right STS and the right subgenual ACC (see Figure 4A). In contrast, the right STG (66, −32, 20) showed positive connectivity, with an extended bilateral cluster encompassing the voice-selective areas, as well as the left posterior insula and the ACC. Activity of the right STG was negatively correlated with bilateral visual areas and the left MFG. In addition, during Feel Negative, the right ACC seed region showed greater functional connectivity with parts of the pre- and post-central gyri (somatomotor areas), the SMA, the STG and the MTG, whereas the left ACC showed greater functional connectivity with the left STG and Heschl's gyrus and decreased connectivity with areas in the occipital cortex and the cerebellum.

To investigate the network that is specific to reappraisal to increase and decrease negative emotion (Table 6 and Figures 4B–D and 5), we conducted two separate PPIs, selecting a VOI in the left SFG (−16, 38, 42), which was the only significant cluster in the contrast Increase > Decrease, and a VOI in the right MFG (52, 34, 24) for the Decrease > Increase contrast. Using the left SFG as a VOI (Table 6, top and Figure 4B), we found greater functional connectivity during Increase than during Decrease trials, with an extended cluster encompassing lower and higher level right auditory cortices, the left posterior insula, the left STG and the left IFG. For Decrease > Increase, the left SFG was functionally connected to the left middle occipital gyrus. In contrast, the VOI in the right MFG (Table 6, bottom and

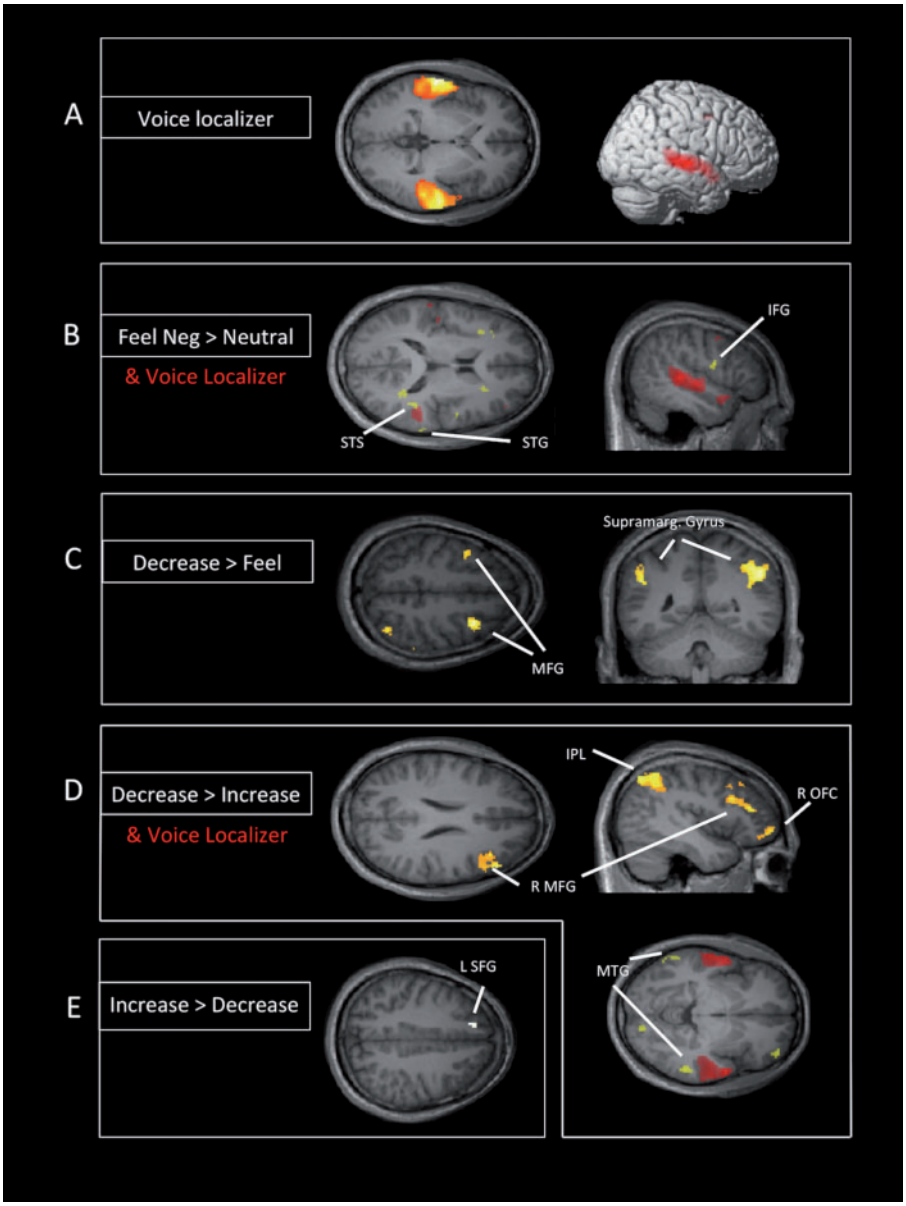

Fig. 3. Relevant activations across contrasts of the voice localizer (A) and main task (B–E). Where relevant, activations of the main task are overlaid on activations of the voice localizer. (B) Listening to angry over neutral prosody without engaging in reappraisal resulted in increased activity in the right STS and STG, as well as in the right IFG. (C) Reappraisal to decrease negative emotions to angry prosody recruited prefrontal and posterior parietal areas in both hemispheres. (D) Decrease > Increase also led to greater activity of the right lateral PFC and OFC. (E) Increase > Increase resulted in a significant cluster only in the left SFG. IFG, inferior frontal gyrus; IPL, inferior parietal lobule; MFG, medial frontal gyrus; MTG, medial temporal gyrus; OFC, orbitofrontal cortex; SFG, superior frontal gyrus; STS, superior temporal sulcus; STG, superior temporal gyrus.

Figure 4C) showed greater connectivity during Decrease compared with Increase trials, with extended bilateral auditory regions encompassing the STG and the MTG (strongly overlapping with the voice-sensitive areas, see Figure 4D), as well as the left dorsolateral PFC (SFG), parietal cortex (superior and inferior parietal lobule) and middle ACC (MFG). The right MFG showed negative functional connectivity during Decrease *vs* Increase trials, with an extended bilateral cluster in the visual cortices, including the cuneus, and the right parahippocampal gyrus.

Discussion

The major aim of this experiment was to investigate whether the reappraisal of auditorily induced negative emotions recruits the same neural network previously reported to underlie the reappraisal of visually induced emotions, as well as whether reappraisal modulates amygdala activity, as has been shown to be the case in the visual domain. Auditory stimuli, consisting of emotional speech spoken with angry prosody (but semantically unintelligible for participants) were paired with written scenarios to evoke negative emotions, while neutral prosody served as control. Across three conditions, participants were instructed to increase or decrease their emotional response to angry prosody by imagining a worsening or improving of a neutral situation described by the combination of a scenario and the auditory stimulus, or in a control condition to pay attention to their emotional response without modifying it.

Table 1. Group activations for Feel Negative > Feel Neutral contrast

Region	Side	Coordinates (MNI)			z score	Cluster size
		x	y	z		
Anterior cingulate	Right	20	−2	32	5.01	353
	Left	−18	14	30	4.98	766
Posterior cingulate	Right	24	−24	28	4.51	70
	Right	32	−64	6	3.54	33
IFG	Right	52	0	20	4.10	44
STS	Right	40	−42	14	3.82	28
STG	Right	66	−32	20	3.41	19
Precuneus	Right	24	−56	34	3.74	29
Inferior parietal lobule	Left	−36	−40	30	3.73	17
	Left	−32	−38	42	3.48	31
Inferior parietal lobule	Right	36	−38	26	3.45	18
Postcentral gyrus	Left	−60	14	26	3.39	20

Note. Clusters of 10 or more contiguous voxels whose global maxima meet a threshold of $P < 0.001$ uncorrected are reported. Regions of activation are listed with best estimates of anatomical location.

Table 2. Group activations for Increase > Feel and Feel > Increase contrasts

Region	Side	Coordinates (MNI)			z score	Cluster size
		x	y	z		
Increase > Feel Negative						
Cuneus	Left	−10	−104	2	3.66	22
Feel Negative > Increase						
Lingual Gyrus	Right	16	−90	−8	4.73	91

Note. Clusters of 10 or more contiguous voxels whose global maxima meet a threshold of $P < 0.001$ uncorrected are reported. Regions of activation are listed with best estimates of anatomical location.

As expected, participants reported stronger negative emotion in response to angry compared with neutral prosody in the Feel condition. In agreement with the results of previous reappraisal studies (e.g. Ochsner *et al.*, 2004), the strength of negative emotions was, moreover, significantly modulated according to reappraisal goals in the Increase and Decrease conditions (see Figure 2). Specifically, negative emotion in response to angry prosody was significantly stronger after reappraisal to increase it than it was after reappraisal to decrease it, with the strength of negative emotion during passive listening in the Feel condition falling in between. However, differences between conditions Decrease and Feel on the one side, and Increase and Feel on the other side, did not reach statistical significance.

As expected, listening to angry compared with neutral prosody in the Feel condition resulted in activation of a right-sided network encompassing the STG, the STS and the IFG (see Figure 3B). This network has also been reported in previous fMRI studies that used emotional prosody (e.g. Grandjean *et al.*, 2005; Frühholz and Grandjean, 2012) and is deemed fundamental for the processing of vocal emotional stimuli (Schirmer and Kotz, 2006; Witteman *et al.*, 2012). The IFG area found here, which is somewhat more posterior compared with that found in earlier studies, belongs to BA 44 and is thus still part of the prosody-processing network (Frühholz and Grandjean, 2013c).

Table 3. Group activations for Decrease > Feel Negative and Feel Negative > Decrease contrasts

Region	Side	Coordinates (MNI)			z score	Cluster size
		x	y	z		
Decrease > Feel Negative						
Middle frontal gyrus	Right	30	12	52	4.63	136
	Right	52	30	28	3.44	15
	Left	−38	6	52	3.40	15
Supramarginal gyrus	Right	50	−48	36	4.46	557
	Left	−50	−48	30	4.04	195
Middle temporal gyrus	Left	−62	−42	−6	3.64	22
	Left	−58	−24	−12	3.44	11
Superior parietal lobule	Right	38	−62	52	3.50	23
Brainstem	Right	2	−16	0	3.97	17
Cerebellum	Left	−10	−40	−22	3.88	36
Feel Negative > Decrease						
Middle occipital gyrus	Right	26	−98	8	4.8	118
Superior front gyrus	Left	−14	36	40	3.63	18
Anterior cingulate	Left	−14	50	2	3.41	13

Note. Clusters of 10 or more contiguous voxels whose global maxima meet a threshold of $p < .001$ uncorrected are reported. Regions of activation are listed with best estimates of anatomical location.

Table 4. Group activations for Increase > Decrease and Decrease > Increase contrasts

Region	Side	Coordinates (MNI)			z score	Cluster size
		x	y	z		
Increase > Decrease						
SFG	Left	−16	38	42	3.26	19
Decrease > Increase						
Middle frontal gyrus/OFC	Right	38	58	−4	4.13	116
Middle front gyrus	Right	52	34	24	4.58	658
	Right	26	52	6	3.34	23
	Left	−42	26	40	4.75	62
Inferior parietal lobule	Right	38	−64	46	4.92	1385
	Right	48	−38	48	3.93	15
	Left	−36	−58	42	4.19	173
	Left	−46	−44	46	3.44	14
Superior parietal lobule	Left	−30	−74	44	3.52	52
Middle temporal gyrus	Right	56	−42	−6	4.04	64
	Left	−64	−50	−4	3.62	78
	Left	−54	−48	−14	4.2	13
Cerebellum	Left	−22	−68	−38	4.25	315
Lingual gyrus	Left	−24	−88	−12	4.10	140
	Right	14	−88	−6	3.88	38

Note. Clusters of 10 or more contiguous voxels whose global maxima meet a threshold of $P < 0.001$ uncorrected are reported. Regions of activation are listed with best estimates of anatomical location.

As shown by PPI analyses (Figure 4A and Table 5), during the perception (without regulation) of angry prosody, functional coupling increased between (i) the right STS, the IFG and the parietal cortex; (ii) between the right STG and the bilateral auditory areas encompassing the voice-sensitive area; (iii) between the right ACC, somatomotor cortices, the STG and the MTG; and (iv) between the left ACC, the STG and Heschl's gyrus. Neutral prosody instead led to greater functional connectivity

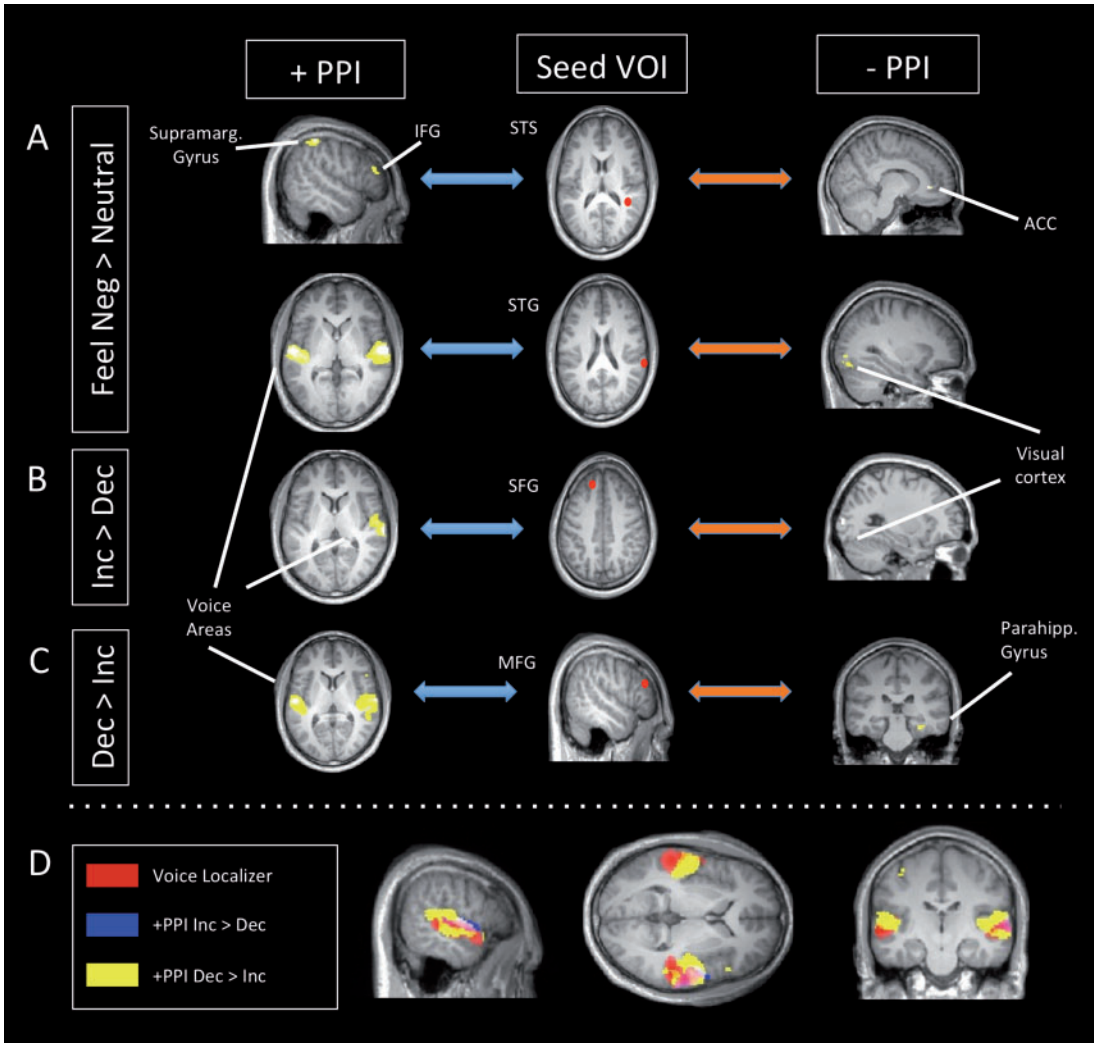

Fig. 4. (A–C) Pattern of increased functional connectivity (left) and inverse functional connectivity (right) with functionally defined seed regions (center), as assessed with PPI analyses. (D) Auditory regions functionally connected with the left IFG during reappraisal to increase negative emotion, and with the right MFG during reappraisal to decrease negative emotion, overlapped with bilateral voice-sensitive areas. ACC, anterior cingulate cortex; IFG, inferior frontal gyrus; MFG, medial frontal gyrus; STS, superior temporal sulcus; STG, superior temporal gyrus; SFG, superior frontal gyrus.

(i) between the right STS and the subgenual ACC, (ii) between the right STG and the extrastriate visual cortices and (iii) between the left ACC and areas in the occipital cortex and the cerebellum. These results are in line with the hypothesis that the clusters in the right STS and the STG are part of a network involved in the processing of emotional aspects of vocal stimuli. Neural activity in these areas appears to be tightly linked, respectively, to the IFG (part of a network implicated in the processing of vocal emotions (e.g. see Schirmer and Kotz, 2006; Frühholz and Grandjean, 2012, 2013c; Witteman *et al*., 2012) and the parietal cortex (likely reflecting the allocation of attentional resources, e.g. see Behrmann *et al*., 2004) on the one hand, and to the extended bilateral auditory cortices (roughly encompassing the voice-sensitive areas) on the other hand. In addition, the STG may be part of a regulatory network that is active during reappraisal (Kohn *et al*., 2014). In addition, the contrast Increase over Feel resulted in a cluster of increased activation in the left cuneus (see Table 2), possibly due to heightened attention to anger prosody during reappraisal to increase. In line with this, Sander *et al*. (2005) reported cuneus activations when anger prosody was attended *vs* unattended to.

Both reappraisal conditions recruited prefrontal areas, but only reappraisal to decrease negative emotion was also accompanied by activations in parietal cortices (Figure 3C–E and Tables 3 and 4). More specifically, the left SFG was more active during reappraisal to increase than to decrease negative emotion. In contrast, reappraisal to decrease emotion revealed activations in mostly right-sided parietal cortices encompassing the inferior and superior parietal lobule, as well as prefrontal areas in the MFG and the OFC. Overall, the pattern reported herein of (i) 'left'-sided SFG activation during Increase conditions and (ii) mostly 'right'-sided activation in the middle frontal gyrus and inferior parietal lobule during Decrease conditions matches the results of previous neuroimaging studies; in addition, this pattern overlaps with the frontoparietal regulation network pinpointed by recent reviews of the reappraisal literature (but see van Reekum *et al*., 2007; Ochsner and Gross, 2008; Kalisch, 2009; Buhle *et al*., 2013; Kohn *et al*., 2014). For example, Ochsner *et al*. (2004) reported a cluster in the left SFG for the contrast Increase > Decrease and for the reverse contrast clusters in the right SFG, MFG and IFG, as well as in the right inferior parietal lobule. Urry *et al*. (2006) reported greater activation in

Table 5. Group activations for PPI analyses on the Feel Negative > Feel Neutral and Feel Neutral > Feel Negative contrasts

Region	Side	Coordinates (MNI)			z score	Cluster size
		x	y	z		
Seed right STS (40 −42 14)						
Feel Negative > Feel Neutral						
Supramarginal gyrus	Right	54	−36	56	5.18	94
	Left	−42	−36	38	4.07	37
IFG	Right	54	34	18	4.39	22
Middle frontal gyrus	Right	50	24	42	3.5	14
	Right	40	14	50	3.38	13
	Left	−54	18	34	3.42	10
Feel Neutral > Feel Negative						
Anterior cingulate	Right	10	36	−2	3.7	40
Seed right STG (66 −32 20)						
Feel Negative > Feel Neutral						
STG	Right	64	−12	2	4.60	1277
	Left	−58	−12	0	4.59	1267
Planum polare (insula)	Left	−40	−2	−12	3.47	14
MFG (ACC)	Left	−4	24	48	3.38	19
Feel Neutral > Feel Negative						
Middle occipital gyrus	Right	26	−94	−6	4.32	119
	Left	−44	−70	−16	4.32	35
	Left	−32	−88	−2	4.24	69
Superior occipital gyrus	Right	20	−90	18	3.30	14
	Right	30	−78	24	3.22	12
Fusiform gyrus	Left	−32	−78	−16	3.81	129
Cuneus	Left	−12	−96	16	3.69	22
	Left	−24	−100	−6	3.46	12
Right calcarine	Right	22	−58	14	3.47	42
Lingual gyrus	Right	4	−76	−6	3.64	68
	Right	8	−88	−4	3.60	66
Middle frontal gyrus	Right	24	14	38	3.64	24
	Left	−36	0	42	3.45	15
Seed right ACC (20 −2 32)						
Feel Negative > Feel Neutral						
Postcentral gyrus (OP)	Left	−50	−14	18	4	56
Postcentral gyrus	Right	60	−12	36	3.56	19
Postcentral gyrus	Left	−54	−22	30	3.43	18
Postcentral gyrus	Left	−44	−20	50	3.36	26
Postcentral gyrus	Left	−56	−28	22	3.29	14
Precentral gyrus	Left	−28	−12	62	3.40	51
Precentral gyrus	Right	30	−10	56	3.38	14
SMA	Left	−12	−12	62	3.95	85
Superior parietal lobule	Left	−16	−58	70	3.89	43
Heschls gyrus	Left	−60	−10	10	3.54	42
STG	Right	60	−16	6	3.48	63
Middle temporal gyrus	Right	70	−34	0	3.46	38
Prefrontal white matter	Left	−28	6	20	3.99	37
Feel Neutral > Feel Negative						
No significant effects						
Seed left ACC (-18 14 30)						
Feel Negative > Feel Neutral						
Heschls gyrus	Left	−62	−12	8	3.66	123
STG	Right	60	−24	4	3.28	18
Feel Neutral > Feel Negative						
Calcarine gyrus	Right	16	−88	4	3.84	344
Middle occipital gyrus	Left	−32	−72	30	3.67	32
Fusiform gyrus	Left	−22	−82	−18	3.51	26
Occipital white matter	Left	−24	−54	20	3.42	12
Cerebellum	Right	14	−70	−28	3.36	27

Note. Clusters of 10 or more contiguous voxels whose global maxima meet a threshold of $P < 0.001$ uncorrected, are reported. Regions of activation are listed with best estimates of anatomical location.

Table 6. Group activations for PPI analyses on the Increase > Decrease and Decrease > Increase contrasts

Region	Side	Coordinates (MNI)			z score	Cluster size
		x	y	z		
Seed left SFG (−16 38 42)						
Increase > Decrease						
STG	Right	66	−24	6	4.25	622
	Left	−60	−32	18	3.65	28
Precentral gyrus	Left	−56	−4	10	3.24	27
Insula	Left	−44	−4	−2	3.72	14
Decrease > Increase						
Middle occipital gyrus	Left	−28	−92	10	3.46	19
Seed right MFG (52 34 24)						
Increase > Decrease						
Cuneus	Right	14	−94	4	4.65	1147
	Left	−12	−98	18	3.50	20
Parahippocampal gyrus	Right	30	−30	−20	4.03	35
	Left	−26	−40	−14	3.47	18
Occipitotemporal gyrus	Left	−46	−58	−8	3.55	17
Decrease > Increase						
STG	Left	−56	−16	4	4.96	1672
	Left	−44	6	−14	3.36	10
	Right	48	14	−10	3.79	78
Middle temporal gyrus	Right	64	−30	0	4.70	2448
SFG	Left	−12	8	66	4.29	83
MFG	Left	−4	16	50	3.84	119
IFG	Right	52	22	6	3.31	10
Paracentral lobule	Left	−44	−40	50	4.04	89
Globus pallidum	Right	24	−8	−4	3.35	11
Precentral gyrus	Left	−38	−18	58	3.31	14

Note. Clusters of 10 or more contiguous voxels whose global maxima meet a threshold of $P < 0.001$ uncorrected, are reported. Regions of activation are listed with best estimates of anatomical location.

the left medial and superior frontal gyri during the reappraisal to increase condition compared with both an attend and a reappraisal to decrease condition. Although it might not be directly related to reappraisal, the neural circuitry underlying the voluntary suppression of unwanted memories shows striking overlap with the reappraisal network, especially in the lateralization of prefrontal areas. For example, Gagnepain *et al.* (2014, see Table S1) found that the voluntary suppression of unwanted memories recruits a mainly right-sided network encompassing the right SFG, MFG and IFG, whereas voluntarily remembering an object associated with a cue leads to increased activity in the left IFG. The agreement between our findings and those reported in the literature suggests that a similar network of prefrontal and parietal areas (the latter specifically for the Decrease condition) allows the reappraisal of negative emotions, irrespective of whether emotional reactions are triggered by using visual (e.g. IAPS pictures) or auditory (i.e. angry prosody) stimuli. Interestingly, the location and lateralization of prefrontal areas recruited during reappraisal to decrease and to increase emotion show similarities with those activated during the suppression and the retrieval of memories.

To explore functional coupling during reappraisal, we performed two separate PPIs by using as seed regions a left and a right prefrontal area, which were among the strongest activations during reappraisal to increase and to decrease negative emotion, respectively (Figures 4B and C and 5 and Table 6). During Increase trials, (i) the activity of the left SFG was functionally related to activation in the right-sided auditory cortices,

the left posterior insula, the left STG and the left IFG; (ii) functional connectivity decreased between the left SFG and occipital areas; and (iii) the right MFG became functionally connected to visual areas and the bilateral parahippocampal gyrus. Decrease trials, on the other hand, were accompanied by (i) greater functional connectivity between the right MFG and the bilateral auditory and parietal areas, the left-sided and medial PFC, and the globus pallidum; and (ii) increased functional connectivity between the SFG and occipital areas (Figure 4C and Table 6). The auditory areas emerging from these PPIs roughly overlapped with the voice-sensitive areas derived from the voice localizer task (Figure 4D).

Although PPI analyses do not reveal the direction of functional connectivity (i.e. which area drives or is driven by the functional interaction), it can be assumed that during reappraisal to increase negative emotion, the left SFG influences activity in the right-sided voice-sensitive areas. Indeed, similar left prefrontal areas were also found to be involved in reappraisal to increase negative emotion induced through visual stimuli (Ochsner *et al.*, 2004; Urry *et al.*, 2006). However, while actively increasing emotions elicited via visual stimuli typically leads to greater amygdala activation, this was not found here. Instead, the increase of auditorily evoked emotions may have been mediated by right lower and higher level auditory cortices, including the regions of the STS and the MTG. Moreover, functional connectivity also increased between the left SFG and the left posterior insula, suggesting that the SFG, as an executive control area, modulates processing in brain areas representing (auditory) sensations.

When compared with the network underlying reappraisal to increase negative emotion, that underlying reappraisal to decrease negative emotion appears to be more complex, as the right MFG becomes functionally coupled with a more extended network, including the bilateral parietal, medial prefrontal and auditory areas. From the extant literature, one can assume that the prefrontal regions in this network drive participants' efforts of emotional down-regulation and therefore influence auditory cortices and related regions of the STS and MTG in a top-down manner, while recruiting attentional resources, as reflected in posterior parietal activations. Moreover, the overall more extended network of functionally connected areas during reappraisal to decrease negative emotion may reflect participants' greater subjective difficulty in decreasing negative emotions than in increasing them, as previously reported (Ochsner *et al.*, 2004); alternatively, participants might not have been as successful in up-regulating compared with down-regulating their negative emotions. In line with earlier reports of increased functional connectivity between various areas of the PFC and the amygdala during reappraisal (Banks *et al.*, 2007), our results showed increased functional coupling between right auditory and bilateral prefrontal areas during both reappraisal to increase and to decrease negative emotions, as well as greater functional connectivity between the left auditory cortices and the right MFG.

Neural activity of the amygdala was not modulated by the angry prosody or participants' reappraisal attempts. First, passive listening to angry prosody did not result in increased activation of the amygdala or the basal ganglia (in both whole-brain and ROI analyses). This null finding stands in contrast to most studies that used visual stimuli to elicit negative emotions and therefore suggests that amygdala activity may be an index of emotional salience of visual stimuli, rather than an index of felt emotion per se (Liberzon *et al.*, 2003; Sander *et al.*, 2003; Lindquist *et al.*, 2012). The result is not entirely surprising; however, since previous brain imaging studies that used prosodic speech stimuli reported inconsistent findings regarding amygdala activation. Although some studies reported amygdala and/or basal ganglia modulation in response to angry prosody (Grandjean *et al.*, 2005; Sander *et al.*, 2005; Frühholz *et al.*, 2012), others did not find increased amygdala activation to emotional prosody (Buchanan *et al.*, 2000; Wildgruber *et al.*, 2002, 2005; Kotz *et al.*, 2003, 2013; Ethofer *et al.*, 2006; Wiethoff *et al.*, 2008; Szameitat *et al.*, 2010; Escoffier *et al.*, 2013). Similarly, lesions of these areas have been reported to result in impairments in the processing of vocal emotions in some patients (Scott *et al.*, 1997), but often fail to be associated with impaired prosody perception (Adolphs and Tranel, 1999; Anderson and Phelps, 2002; Mitchell and Bouças, 2009; Bach *et al.*, 2013). For example, Grandjean *et al.* (2008) studied the effects of emotional prosody on auditory extinction in six right-hemisphere patients and found that lesions in the caudate, OFC and superior temporal cortex (but not the amygdala) were associated with reduced sensitivity to emotional prosody. In another study, amygdala lesions due to an anterior temporal lobectomy were also found to affect emotion perception more in the visual than in the auditory domain (Milesi *et al.*, 2014). More research is thus needed to understand if and how the amygdala might be involved in the response to emotional prosody. However, at least some of these inconsistencies in the literature may be related to the type and length of the stimuli used. The rather long vocal stimuli used in our study may have caused amygdala habituation (Zald, 2003).

Thus, despite angry prosody inducing negative emotions as suggested by participants' ratings (Figure 2), this subjective emotional response did not increase the BOLD signal within the amygdala or the basal ganglia—which may be due to habituation to the comparatively long auditory stimuli. Instead, the increased activity of higher auditory regions of the right STS and STG, as well as the IFG, reported herein may be related to the generation of negative emotional responses to vocal stimuli, in addition to being the substrate for the processing of speech prosody (Frühholz and Grandjean, 2013b,c). However, ROI analyses on the average activation of the left and right voice areas (determined with the voice localizer task) did not result in significant modulation by angry prosody (there was, however, a non-significant trend for the Increase > Feel Neutral difference in the right voice area). The reason for this null effect may be that averaging over such extended areas as the entire voice area (encompassing a big chunk of the STS and STG) occluded their stimulus and/or task-driven modulation.

Second, amygdala activity did not change depending on reappraisal to increase or decrease negative emotions elicited by the angry prosody. No significant clusters of activation in the amygdala emerged from whole-brain analyses (or PPI analyses). Moreover, even though ROI analyses on the amygdala resulted in a significant Condition × Side interaction, none of these differences reached significance or trend level when tested with paired-samples *t*-tests. We conclude that no modulation of the amygdala occurred on the basis of the emotional character of the stimulus (Anger *vs* Neutral) or on the basis of participants' cognitive effort during reappraisal (Increase and Decrease *vs* Feel).

Heart rate was measured throughout the task, but did not differ between angry and neutral prosody, nor was it significantly modulated by reappraisal to increase or decrease negative emotion. Greater heart rate in response to angry than in response to neutral prosody had been expected, based on the frequent finding of increased heart rate in response to anger stimuli (Kreibig, 2010). However, a

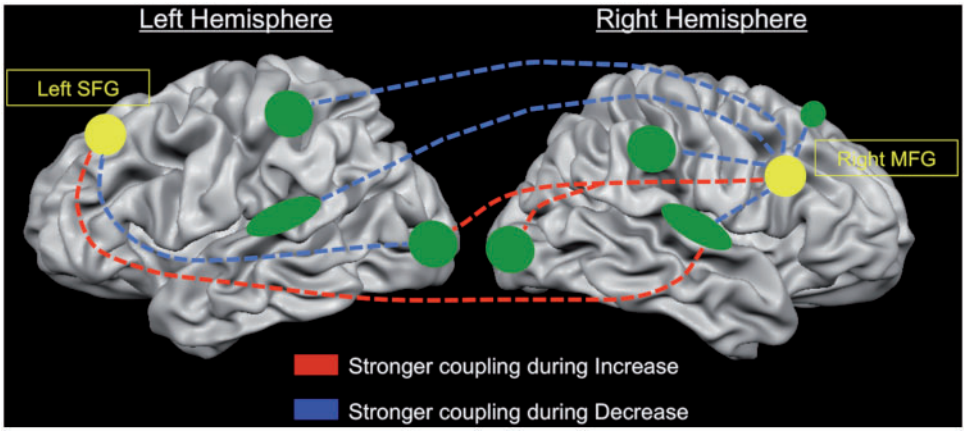

Fig. 5. Representation of the most important areas of increased functional connectivity during Increase (red arrows) and Decrease (blue arrows) conditions, respectively, using as seed regions the left SFG and the right MFG.

recent study specifically investigating the effects of emotional prosody on peripheral physiology similarly failed to find a modulation of heart rate (Aue *et al.*, 2011). Therefore, on the basis of these results and the most recent literature, angry prosody does not, in contrast to visual stimuli (e.g. IAPS pictures), reliably modulate the BOLD signal within the amygdala, or lead to increased heart rate. From the study results reported by Aue *et al.* (2011), other physiological parameters, such as skin conductance and forehead temperature, might be more sensitive to the cognitive and affective reactions to angry *vs* neutral prosody. Another reason for the lack of results on HR is that, given the variety of negative emotions that scenarios and anger prosody could elicit, changes in HR might have cancelled each other out. For example, HR might have decreased for trials inducing embarrassment, but increased for those triggering fear or anger.

Confounds, limitations and future directions

A condition requiring the reappraisal of neutral prosody was not included, because we reasoned that reappraisal works best when an emotional reaction has started occurring. In other words, it would have been difficult to instruct participants to increase or decrease their emotions if they had no emotions in the first place. Many other reappraisal studies also lacked a condition requiring the reappraisal of neutral stimuli (Ochsner *et al.*, 2002), or included it but did not analyze such trials (Ochsner *et al.*, 2004).

Similar reasoning led us to present short scenarios before the auditory stimuli in order to provide a context for the stimuli. Our goal was to use scenarios that were as neutral as possible, but nevertheless could plausibly be followed by an angry voice stimulus. The reason for choosing this combined scenario-prosody paradigm was that the voice stimuli by themselves were difficult to reappraise because they were in Italian and therefore their semantics could not be understood. In line with previous reappraisal experiments, we provided a short training session but did not control for (intra- and interindividual) differences in the ability to imagine the scenarios. This can be seen as a possible confound because some participants may have been better able to imagine the scenarios and therefore to have stronger emotional reactions. Nevertheless, subjective ratings of felt emotion differed between conditions when averaging over all participants, suggesting that the scenario-prosody combination generally induced the expected emotions.

Gender differences have been shown to occur at several levels of the emotional response (Eisenberg and Lennon, 1983; Dimberg and Lundquist, 1990; Kring and Gordon, 1998), as well as for the neural correlates of emotion regulation in response to visual stimuli (McRae *et al.*, 2008). It is therefore possible that the neural correlates of voluntary reappraisal of angry prosody also differ between men and women. The current experiment was not designed to address these gender differences, and the sample size, and consequently the statistical power of the analyses, is considerably reduced when splitting the data into a group of eight men and 10 women. We have nevertheless run the second-level fMRI model separately by gender, which resulted in similar, albeit weaker, brain activation patterns in female participants, but in few significant activations in male participants. In light of the decrease in statistical power when analyzing such reduced groups of participants, we are reluctant to interpret these group differences as an effect of gender, and we suggest that future studies investigate these issues more specifically.

The left dominance for reappraisal to increase negative emotion and the right dominance for reappraisal to decrease negative emotion reported herein is in line with the brain-imaging literature on emotion regulation and has been explained by the different cognitive processes involved (Ochsner and Gross, 2005). However, alternative hypotheses exist pertaining to motivational tendencies and global-local processing of information.

For example, it may be that this asymmetry reflects participants' felt emotions and behavioral tendencies, rather than, or in addition to, their reappraisal efforts. Previous research (using EEG and power in the Alpha band as a proxy of neural deactivation) has suggested that approach motivation (typical for anger, among other things) is characterized by relatively increased left prefrontal brain activation, whereas withdrawal motivation (typical of basically all negative emotions besides anger) is caused and/or accompanied by relatively increased right PFC activation (Davidson, 1998; Harmon-Jones, 2003; Harmon-Jones *et al.*, 2010). Increase trials may have led to stronger feelings of anger (an approach motivation), whereas Decrease trials may have caused reduced anger but increased feelings of remorse (a withdrawal motivation). In other words, the left-lateralized prefrontal activity during reappraisal to increase negative emotion

and the right-lateralized activity during reappraisal to decrease negative emotion could be explained by the outcome of the reappraisal (approach *vs* withdrawal motivation), rather than by the reappraisal itself. It needs to be emphasized; however, that this interpretation holds true only when assuming these exact emotional and motivational outcomes. Other likely outcomes of reappraisal, e.g. greater fear (or any other withdrawal motivation) after reappraisal to increase emotion, and less fear (or any other negative emotion with the exception of anger) after reappraisal to decrease emotion, should have resulted, on the basis of the alpha-asymmetry model, in the opposite lateralization of prefrontal areas. Moreover, participants' self-reports suggest that their felt negative emotions were significantly lower in the Decrease compared with the Increase condition, which in terms of prefrontal asymmetry should have resulted in greater left activation in the former and greater right activation during the latter type of reappraisal (except for anger). Nevertheless, the question of what exactly drives prefrontal asymmetry during reappraisal merits further investigation. So far, little is known about the EEG correlates of reappraisal in terms of prefrontal alpha asymmetry. Interesting and promising results were reported by Parvaz *et al*. (2012), who found a significant decrease in left-prefrontal Alpha during the reappraisal to decrease one's emotional response to negative pictures. However, future studies should test, using EEG and more precise measures of participants' emotions before and after reappraisal, whether prefrontal lateralization is due to the direction of the reappraisal effort, or to the nature of the resulting motivational tendencies.

A further possibility that future studies might want to examine is whether reappraisal to increase emotion is associated with greater attention to local features of hierarchical targets and reappraisal to decrease emotion is associated with a more global focus of attention. This hypothesis is based on findings suggesting that the processing of global features is supported by the right central-parietal hemisphere, whereas the processing of local features is associated with the left central-parietal hemisphere (Robertson and Lamb, 1991; Förster and Dannenberg, 2010). In addition, it has been suggested that emotions with high motivational intensity (with clear approach/avoidance motivations) lead to both a more narrow cognitive scope and relatively greater left prefrontal activity, whereas emotions with low motivational intensity are associated with both a broader cognitive scope and relatively increased right prefrontal activation (Harmon-Jones *et al*., 2012).

Conclusions

We have tested, for the first time, the neural network underlying reappraisal of auditorily evoked negative emotions. In accordance with prior studies that used visual stimuli, our study suggests that a network of the right MFG, the OFC and the bilateral posterior parietal cortices underlies the reappraisal to decrease the intensity of felt negative emotions and that the left SFG accompanies reappraisal to increase negative emotions. However, in contrast to results of previous studies that used visual stimuli, amygdala activation was not increased in our study in response to emotional auditory stimuli, and the likely target of these regulatory prefrontal areas was instead the auditory cortices. Right auditory areas showed increased functional connectivity with prefrontal regulatory areas during both reappraisal conditions, whereas left auditory cortices became functionally connected to the right MFG only during reappraisal to decrease negative emotion.

We conclude that a left prefrontal, and a mainly right-sided prefrontal-parietal network, mediate reappraisal to increase and to decrease negative emotions, respectively, independently of the visual or auditory stimulation modalities.

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Appendix

Eighty Scenarios Presented (Originals in French)

N°	Gender	Scenario in English
1	f	In the supermarket, you jump ahead a woman in the queue for the cashier. The woman speaks to you and says:
2	f	At the theater, you jump ahead of a woman in the queue for the cashier. The woman speaks to you and says:
3	m	You meet your neighbor in the staircase of your building. The evening before, you had organized a party. The neighbor speaks to you and says:
4	F	Going to work by bike, you cut across the path of a lady who is walking. The lady speaks to you and says:
5	f	You walk your dog, which poops in a private garden. At that moment, a woman comes out of the house. She speaks to you and says:
6	m	On the subway, a man turns to you and says:
7	f	On the bus, a woman turns to you and says:
8	f	In the street, a woman suddenly turns to you and says:
9	m	You refuse to give alms to a beggar in the street. The beggar tells you:
10	m	When paying for a taxi, you realize that you do not have enough to pay. The driver tells you:
11	m	At the bar, you discuss politics with a person sitting next to you. The man tells you:
12	m	This year, your business expenses were important. You present the amount to your supervisor. The supervisor tells you:
13	m	At the grocery store, you make a remark about the bad quality of the fruits. The grocer tells you:
14	m	You have a meeting with your supervisor. The supervisor tells you:
15	f	A friend lends you his car. You return it with a scratch. The friend tells you:
16	f	A friend lends you a CD, which you return scratched. The friend tells you:
17	m	A friend lends you a book that he likes, but you lose it in the tram. The friend tells you:
18	f	A friend reveals a secret, begging you not to tell anyone. The following day, while you tell the secret to other people, you notice your friend behind you. She tells you:
19	f	In the bus, you step on the toes of a well-dressed lady. The lady tells you:
20	m	You invite a friend to come to your house. When he arrives at your door you tell him that you have to leave due to another appointment. The friend tells you:
21	f	You forget an appointment with your mother, who calls you the next day and tells you:
22	m	You forget an appointment with your father. He calls you the same evening and tells you:
23	f	You park you car in a place where a woman was about to park. The woman speaks to you and says:
24	m	You forget your father's birthday. He points it out to you, saying:
25	f	You receive a gift from a friend. She discovers that you threw it away. She tells you:
26	f	You borrow the computer of a colleague. Without doing it on purpose, you erase some important documents. Now, you have to give the computer back and explain the accident. The colleague tells you:
27	m	Trying to jump ahead in the queue to the ski lift, you walk over the skis of a man. The man tells you:
28	f	You are saying bad things about an acquaintance, when you realize she is just behind you. The woman tells you:
29	f	By email, you make jokes with a friend and talk badly about a colleague. By mistake, the email also goes to this colleague. Soon afterwards, she calls you and tells you:
30	f	You put your desk in order at work. The noise that you are making disturbs a colleague, who tells you:
31	m	You are driving in a hurry and cut the right of way to a scooter. At the next traffic light, the man on the scooter comes next to your window and tells you:
32	m	You put loud music on, even though the neighbor asked you to turn it down. At that moment, the doorbell rings. You open the door and the neighbor tells you:
33	f	In the tram, you listen to loud music on your iPod. A woman turns to you and tells you:
34	m	You are at the theatre. Your mobile phone starts ringing. A spectator sitting in front of you turns around and tells you:
35	f	By mistake, you jostle a lady at the supermarket. Trying to keep her balance, she knocks a few bottles from a shelf. She turns around and tells you:
36	f	Passing through the crowd at a concert, you spill your beer on the jacket of a girl. The girl turns around and says:
37	f	You are working in an open space. At lunch, you warm up some food, which has a strong smell. A colleague tells you:
38	m	Unintentionally, you pour coffee on the white shirt of a colleague. Your colleague tells you:
39	f	You light a cigarette where it is forbidden to smoke. A woman tells you:
40	m	You organize a BBQ at the park with friends. Grilling is forbidden at the park and soon the park ranger comes. He tells you:
41	f	A friend asks you to take care of her plants while she is on vacation. When she comes back, she discovers that several plants have died. She tells you:
42	f	A friend asks you to take care of her aquarium while she is gone. When she comes back, she discovers that several exotic fish have died. She tells you:
43	f	You wash a cashmere sweater in the washing machine. The friend to whom the sweater belongs discovers it has shrunk. She speaks to you and says:

(continued)

(continued)

N°	Gender	Scenario in English
44	f	You wash a white sweater in the washing machine. The friend to whom it belongs discovers its color has changed. She speaks to you and says:
45	f	Unintentionally, you pour tea on some important documents of a colleague. The colleague tells you:
46	m	You are asked to send an important message to your boss. Because you are so busy, you do not write it down and totally forget to send it. The next day, the boss calls you into his office and tells you:
47	f	Your mother asks you to buy food for the meal, but on arriving home, you admit to her that you have forgotten the main ingredient. Your mother tells you:
48	m	Your boss asks you to mail an important letter. You admit to him that you have forgotten to do so. The boss tells you:
49	f	You cut a friend's hair. When she looks into the mirror, she discovers that you cut too much on one side. She tells you:
50	f	To welcome your guests, you offer them a bottle of champagne. Shortly afterward, your roommate, to whom the bottle belonged, comes back home. She tells you:
51	f	By mistake, you mix dirty and clean dishes. Your roommate tells you:
52	f	You forget to wash up for several days in a row. Your roommate tells you:
53	m	You promised your parents to be present at a family reunion. Your father finds out that you have changed your mind and plan to go on vacation instead. Your father says:
54	m	A friend lends you his bike. Stopping at a store, you do not lock the bike properly. You admit the theft of the bike. The friend tells you:
55	f	You order food over the phone. When the delivery woman arrives, you tell her that you do not want it anymore. She tells you:
56	m	During a hike, you camp in a national park, even though it is forbidden. In the morning, a park ranger wakes you and says:
57	m	You cross the road against a red light. A man sees this and tells you:
58	m	You play and win a board game. One of the losing players discovers that you cheated and tells you:
59	m	At the park, you play and win a game of chess against an unknown man, who does not like to lose. He tells you:
60	f	You are planning to go out at night with a group of friends. Another friend finds out that she is not invited and tells you:
61	m	You go to get your mail and start reading a letter in front of the mailboxes. A neighbor is waiting for you to leave and tells you:
62	f	You talk aloud in the street, without noticing that a woman is right behind you. She tells you:
63	m	On your way home after a party late at night, you walk a bit too close to a man in the street. The man turns around and tells you:
64	m	Coming home drunk at night, you make noise and wake up your roommate, who gets up to talk to you. He says:
65	m	At the supermarket, you mistakenly put your things into another person's cart. The person tells you:
66	m	You are on vacation and light some fireworks for your birthday. In the garden next door, your neighbors are eating with friends. The neighbor gets up and tells you:
67	m	A friend lends you his apartment in a foreign city. You bring the trash out to the curb, when the concierge sees you from the window. He comes out and tells you:
68	f	In the queue at the airport, you joke with friends about the clothes of a woman in front of you. Contrary to what you think, this woman understands your language. She turns to you and says:
69	m	At the park, you play soccer with friends using a child's ball. The father of the child comes to talk to you and tells you:
70	m	While Although opening the lock of your bike, you put your bag on a scooter parked next to it. The scooter's owner comes out of the building in a hurry and tells you:
71	m	At an art show, you step out on the street smoking and conversing. You put your glass on the roof of a parked car, without noticing the man inside. The man steps out of the car and tells you:
72	m	You are having a picnic in a farmer's field. The farmer comes by in his tractor and sees you. He comes closer and tells you:
73	m	You are on vacation in a foreign country and you step into the bus from the rear door. The driver speaks into the microphone and tells you:
74	m	You are walking in the street and you pick some berries from the garden of what looks like an empty house. A man jogs by and tells you:
75	f	You are at the bank waiting for a teller without respecting the usual distance to the customer before you. The woman in front of you turns around and says:
76	f	You walk down the stairs of your building while the concierge is cleaning with a mop. She tells you:
77	m	At the park, your son plays with the leaves that a gardener swept together. Another man walks by and tells you:
78	f	You are blocking the sidewalk while talking with friends. A woman is trying to pass with a stroller. She says to you:
79	m	You are in a crowded train and the conductor is asking for the ticket. You take a long time searching for it in all your pockets and bags, when the conductor tells you:
80	f	You spit on the ground while riding your bike, without noticing a woman just behind you. The woman tells you: